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## The effect of temperature on the life cycle of *Drosophila acutilabella*

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THE EFFECT OF TEMPERATURE  
ON THE LIFE CYCLE OF  
DROSOPHILA ACUTILABELLA

A Thesis

Presented to

The faculty of the  
Graduate School of the  
University of the Pacific

In Partial Fulfillment  
of the Requirements of the Degree  
Master of Science

by

Donald A. Miles

Sept. 1981

This thesis, written and submitted by

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## INTRODUCTION

This is a study of the rate of development of the fly, Drosophila acutilabella, Stalker (1953), at three temperatures: 22°, 25° and 28° C. It is part of a larger project testing the hypothesis that stenothermal species (those restricted to a narrow temperature range) are more sensitive than eurythermal species, such as the cosmopolitan D. melanogaster and D. hydei (those able to live over a broad temperature range) to the effects of temperature during development. It has been suggested that eurythermal species have a lower  $Q_{10}$  of development (Hunter, 1968). The species used in this study is considered to be stenothermal because it is limited in distribution to Florida, Cuba, Hispaniola and Jamaica (Wheeler, 1970), which are regions of relatively warm temperature with little seasonal change.

Ectothermic animals, including insects depend primarily on external sources for body heat (Schmidt-Nielsen, 1975), but body temperature is not necessarily equal to the ambient temperature (Prosser, 1973). Endothermic animals regulate body temperature by internal heat production, and can main-

tain relative constancy of body temperature by altering insulation, circulation and other modifiers of heat transfer (Prosser, 1973). In any case, temperature limits the distribution of animals, and at the same time, determines their activity. In general, most life activities occur within the range from about 0° to 40°C, and most animals live within much narrower limits. Limits for reproduction are narrower than those for survival of adults, but the early stages (egg, larva, pupa) of many endotherms tolerate a wider range than do adults.

The "vinegar" flies of the genus Drosophila are convenient animals to use in studies of the effect of temperature on ectotherms. This genus is distributed throughout the world, but some species have a much broader range than others. Most of the species are tropical or semi-tropical and only a few are found in colder areas such as the mountain masses and Arctic regions. For example, 243 species of this genus occur in the Hawaiian islands, El Salvador has at least 100 species, while Alaska has only 9 species (Spieth and Heed, 1972).

Ecological studies indicate that woodland areas are the natural habitat of the vast majority of Drosophila. The cactus-dependent members of the repleta species group have invaded arid and semiarid areas. No Drosophila are known to occur in grasslands and tundra. The adults are diurnal and



display relatively short periods of activity during each morning and evening in their visits to feeding and courtship sites (Spieth and Heed, 1972). Activity periods are usually shorter and more precisely defined in cooler climates than in tropical rain forests and are influenced by light intensity, temperature, and relative humidity, with species-specific differences as to which is the major controlling factor. During the remainder of the day and night individuals appear relatively inactive in hidden, secluded sites scattered throughout their habitat. Food sites, especially tomato fields, orchards, large semi-covered garbage cans, and waste fruit dumps are places where most cosmopolitan species will persist for prolonged periods.

As holometabolous insects, all Diptera have two distinct active life forms, the larva and adult with a quiescent pupal stage between them. The life cycle of Drosophila begins with the fertilized egg, from which the larva emerges. The larva undergoes two molts, shedding its cuticle, mouth hooks, and spiracles. Thus, the larval period consists of three instars. When the larvae are preparing to pupate, they creep from the substrate, and adhere to some relatively dry surface. Drosophila pupate within the last larval skin, which is at first soft and white but slowly hardens and darkens to

become the puparium in which the metamorphosis occurs. When the changes have been completed, the adult emerges (ecloses) by forcing its way through the anterior end of the pupal case or operculum. After the adult fly, or imago, emerges, it matures sexually, mates, lays fertile eggs and the cycle is begun again.

Within viable limits, the duration of each stage of the cycle decreases as the temperature increases. At 20° C the average length of the egg to larval period of development of D. melanogaster is 8 days; at 25° C, it is reduced to 5 days. The pupal life at 20° C is about 6.3 days, whereas at 25° C it is about 4.2 days. Thus, at 25° C the life cycle may be completed in about 10 days, but at 20° C about 15 days are required (Demeree and Kaufmann, 1965). Budnik, Santibanez and Brncic (1971), found that the mean developmental rate for D. pavani from egg to adult was 40.2 days at 16° C and only 18.8 days at 25° C.

In an analysis of the frequency of heterokaryotypes in relation to rate of development, Budnik, et. al. (1971), incubated equal numbers of D. pavani eggs at 16° and 25° C. At both temperatures two groups were established, according to their emergence after the eggs were collected: those of "fast" development (29 to 35 days at 16° C, 14 to 16 days at 25° C), and those of "slow" development (44 to 65

days at 16° C, and 21 to 29 days at 25° C). The rapidly developing flies showed a higher frequency of heterokaryotypes in the left and right arms of the fourth chromosome than the slower ones. This difference was significantly smaller among those flies raised at 25° C.

Tantawy, et. al. (1973) observed significant effects of temperature and genotype in natural populations of D. melanogaster. They observed cases of genotype-genotype or genotype-cytoplasm interactions: heterosis, or hybrid vigor, of the F<sub>1</sub> generation, was manifested clearly at 28° C and less so at 15° C or 25° C. This phenomenon became diminished in the F<sub>2</sub> and in subsequent segregation generations. An intermediate degree of heterosis, as seen in F<sub>1</sub> generations was observed in various backcross generations. This gene-environment interaction varied from population to population.

Armstrong (1976) studied the effects of various temperatures on adults of D. willistoni infected with the sporozoan Nosema kingi. The minimum and maximum temperatures for normal development of both host and parasite were 15-19° and 25-29° C, respectively. The optimum for rearing both host and parasite appeared to be 20-24° C, since their lifespans were longest at these temperatures.

Generally, the adult lifespan of D. willistoni decreased as the temperature increased.

There are many investigations, in addition to those reported here, which demonstrate the effect of different environmental factors on the rate of development. Therefore, it is necessary to control as many factors as possible in any study of the rate of development. It is hypothesized that under controlled conditions, when developing within the viable temperature range (22-28°C), D. acutilabella will have a lower Q<sub>10</sub> of the rate of development than will eurythermal species such as D. melanogaster.



## MATERIALS AND METHODS

Drosophila acutilabella were collected in Pompano Beach, Florida at a temperature of 25°C by Alice S. Hunter. A stock supply was maintained in a 25° ± 1° C incubator. The flies were kept in 80 ml plastic vials with 5 gm of instant Drosophila Medium-Formula 4-24 (Carolina Biological Supply) hydrated with 15 ml of tap water. Vials were stoppered with sterile cotton, which reduced the incidence of mites. The incubators were on a daily light schedule of twelve hours from 7 a m to 7 p m. Milk cartons filled with tap water were placed inside to provide moisture. At the peak of larval activity, pieces of dry paper towel were placed directly on the medium. This provided a site for larvae to pupate.

Pilot studies with D. acutilabella at room temperature showed that they eclosed most actively during mid-afternoon. Newly emerged adults were collected daily from the stock supply between 1 and 4 p m in the afternoon. The adults were then etherized, sexed under a microscope and used in the experiments. Other pilot studies indicated that 22° to 28°C was the optimal temperature range for growth. A wider temperature range was tried (20° to 30°C); however, development

ceased at the pupal stage at the lower and higher temperature.

Experimental vials were set up in the same manner as stock vials except that the surface of the medium was darkened with a solution of yeast and food coloring. This solution was made by adding 3.5 gm ( $\frac{1}{2}$  package) of baker's yeast and approximately 10 ml of green food coloring. A few drops of solution were added to the surface of the medium to provide a background for observing eggs and larvae and to provide yeast for the adult flies.

Eclosion to sexual maturity was the first stage of the life cycle of D. acutilabella measured. Virgin males and females were collected from the stock supply. Four ( $\pm 1$ ) females and eight ( $\pm 1$ ) males were placed in each of twenty vials arranged in groups of four. At 12 hour intervals, beginning after 24 hours, one group of flies was removed from the vials and sexed. Only the females were returned to the vials so that they could deposit eggs. Another group of vials was treated in this manner after 36 hours, 48, 60 and 72 hours. The appearance of larvae and/or pupae was used as evidence of sexual maturity because the females lay unfertilized eggs. If sexual maturity occurred after 60 hours, for example, no larvae or pupae would appear in vials from which males were removed after 36 and 48 hours.



This procedure was repeated with flies at 22°, 25° and 28° C. The vials were checked for appearance of larvae and/or pupae every 12 hours at 7 am and 7 pm.

The other stages in the life cycle were measured at 22°, 25° and 28° C with six pairs of virgin males and females in each of four vials at every temperature. After three days, the six pairs of flies were passed to new vials every 24 hours, until at least 24 empty vials were accumulated at each temperature. The development of the eggs in each vial was followed thereafter. Vials were checked at 12 hour intervals at 7 am and 7 pm for the onset of each stage (larva, pupa, eclosion). The time and date of onset of the stages were recorded.

The  $Q_{10}$  was calculated from the formula:

$$Q_{10} = \left( \frac{K_1}{K_2} \right)^{10/|t_1 - t_2|}$$

where  $K_1$  and  $K_2$  are velocity constants corresponding to temperatures  $t_1$  and  $t_2$  respectively.

The Kruskal-Wallis non-parametric analysis of variance was the statistical analysis used (Book, 1977). The least significant difference test was used to determine the differences between means (Mendenhall, 1977).

## RESULTS

Tables 1 through 3 present the data for the development of D. acutilabella at 22°, 25° and 28° C. Figure 1 is the frequency distribution (Mendenhall, 1977) for the overall lifespan at each temperature. Figures 2 through 4 are frequency distributions for each stage at each temperature.

### Overall Lifespan

The mean minimal duration of the overall lifespan of D. acutilabella at 22°C is  $17.0 \pm 0.8$  days,  $13.0 \pm 0.4$  days at 25°C and  $11.0 \pm 0.4$  days at 28°C ( $P=.01$ ). All means are significantly different from each other.

### Egg to Larva

The mean minimal duration to the egg to larval stage for D. acutilabella is  $2.0 \pm 0.5$  days at 22°C,  $0.9 \pm 0.2$  days at 25°C and  $0.9 \pm 0.1$  days at 28°C ( $P=.01$ ). The means obtained at 25° and 28° C are not significantly different ( $P=.01$ ). The means obtained at 22° and 25° C differ significantly.

### Larva to Pupa

The mean minimal duration of the larval to pupal stage for D. acutilabella is  $5.0 \pm 0.8$  days at 22°C,  $4.0 \pm 0.7$  days at 25°C and  $3.8 \pm 0.4$  days at 28°C ( $P=.01$ ). The means obtained at 25° and 28° C are not significantly different from each other.

The means obtained at 22° and 28° C, however, differ significantly from each other ( $P=.05$ ).

#### Pupa to Eclosion

The mean minimal duration of the pupa to eclosion stage is  $8.6 \pm 0.4$  days at 22° C,  $6.2 \pm 0.4$  days at 25° C and  $5.2 \pm 0.3$  days at 28° C ( $P=.01$ ). All means are significantly different from each other ( $P=.05$ ).

#### Eclosion to Sexual Maturity

The mean minimal duration of the eclosion to sexual maturity stage is 1.5 days at 22° C, 2.0 days at 25° C and 1.5 days at 28° C. The means are not significantly different from each other ( $P=.01$ ). In this case, at all three temperatures the sample sizes were too small to measure deviation from the mean and standard error.

#### Q<sub>10</sub> values

The Q<sub>10</sub>'s are calculated for the mean minimal duration of the overall lifespan. The Q<sub>10</sub> value for 22° to 25° C is 2.4, for 25° to 28° C it is 1.6 and for the entire temperature range, it is 2.0.

TABLE 1

Duration of the stages in the life cycle of  
D. acutilabella at 22°C (in days)

| Statistic  | Overall<br>Life Cycle | Egg to<br>Larva | Larva to<br>Pupa | Pupa to<br>Eclosion | Eclosion to<br>Sexual Maturity |
|------------|-----------------------|-----------------|------------------|---------------------|--------------------------------|
| Mean       | 17.0                  | 2.0             | 5.0              | 8.6                 | 1.5                            |
| Std. dev.  | 1.3                   | 0.8             | 1.5              | 0.7                 | ----                           |
| Std. error | 0.3                   | 0.2             | 0.3              | 0.1                 | ----                           |
| % of cycle | 100                   | 11.7            | 29.2             | 50.3                | 8.8                            |
| N          | 22                    | 24              | 24               | 22                  | 2                              |

TABLE 2

Duration of the stages in the life cycle of  
D. acutilabella at 25°C (in days)

| Statistic  | Overall<br>Life Cycle | Egg to<br>Larva | Larva to<br>Pupa | Pupa to<br>Eclosion | Eclosion to<br>Sexual Maturity |
|------------|-----------------------|-----------------|------------------|---------------------|--------------------------------|
| Mean       | 13.0                  | 0.9             | 4.0              | 6.2                 | 2.0                            |
| Std. dev.  | 0.7                   | 0.4             | 1.1              | 0.6                 | ----                           |
| Std. error | 0.1                   | 0.1             | 0.2              | 0.1                 | ----                           |
| % of cycle | 100                   | 6.5             | 30.3             | 47.5                | 15.4                           |
| N          | 24                    | 25              | 24               | 24                  | 3                              |

TABLE 3

Duration of the stages in the life cycle of  
D. acutilabella at 28°C (in days)

| Statistic  | Overall<br>Life Cycle | Egg to<br>Larva | Larva to<br>Pupa | Pupa to<br>Eclosion | Eclosion to<br>Sexual Maturity |
|------------|-----------------------|-----------------|------------------|---------------------|--------------------------------|
| Mean       | 11.2                  | 0.9             | 3.8              | 5.2                 | 1.5                            |
| Std. dev.  | 0.8                   | 0.2             | 0.8              | 0.5                 | ----                           |
| Std. error | 0.2                   | 0.1             | 0.5              | 0.1                 | ----                           |
| % of cycle | 100                   | 8.2             | 34.1             | 46.4                | 13.4                           |
| N          | 23                    | 25              | 24               | 20                  | 3                              |



Figure 1 - The frequency distribution of the overall lifespan of D. acutilabella at (a) 22°C, (b) 25°C and (c) 28°C.

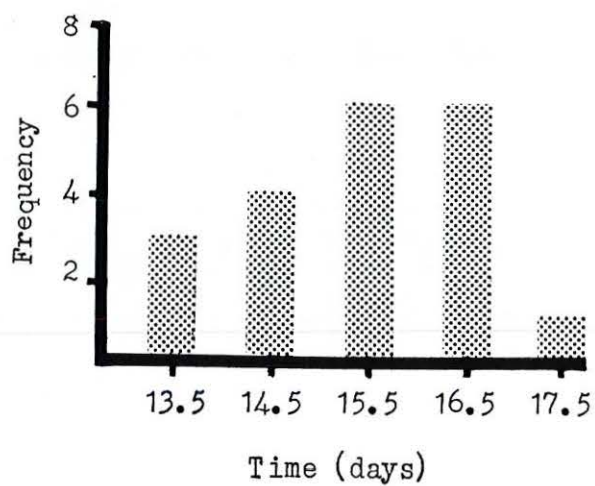
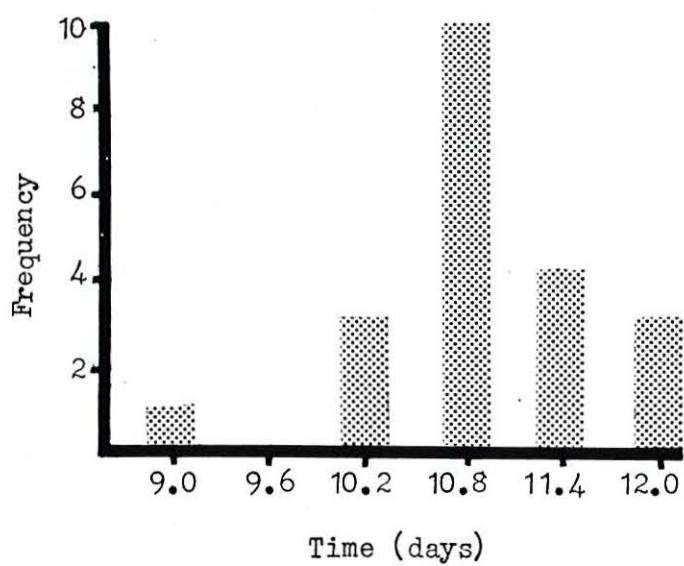
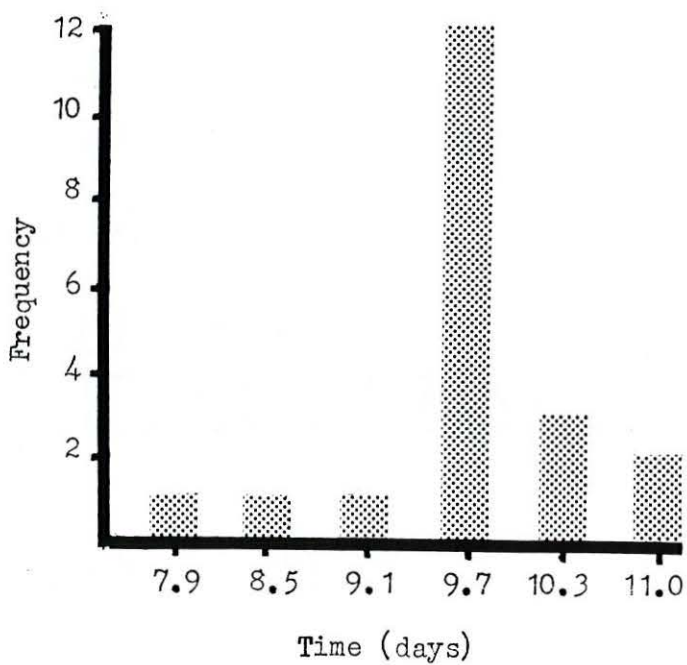
Fig. 1a: 22°CFig. 1b: 25°CFig. 1c: 28°C

Figure 2 - The frequency distribution of the egg to larval stage of development for D. acutilabella at (a) 22°C, (b) 25°C and (c) 28°C.

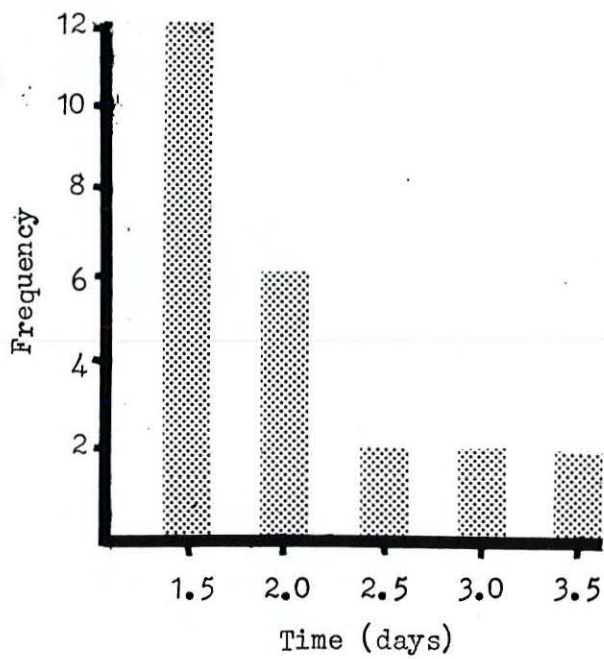
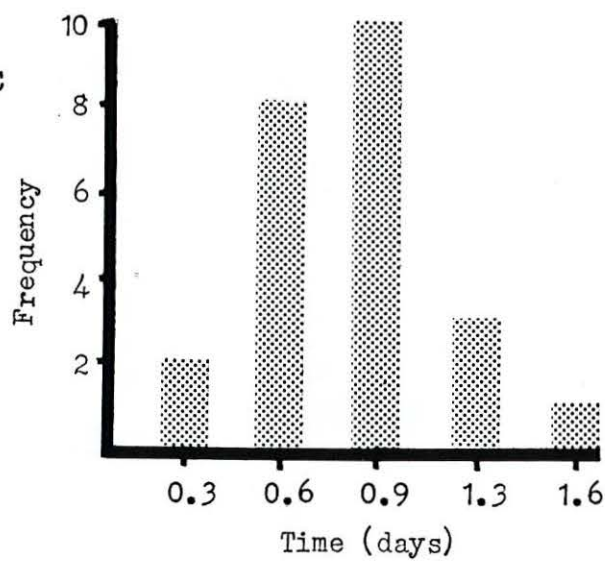
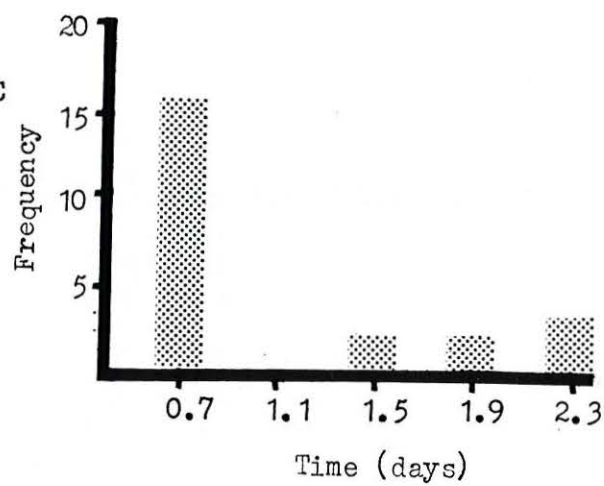
Fig. 2a: 22°CFig. 2b: 25°CFig. 2c: 28°C

Figure 3 - The frequency distribution of the larval to pupal stage of development for D. acutilabella at (a) 22°C, (b) 25°C and (c) 28°C.

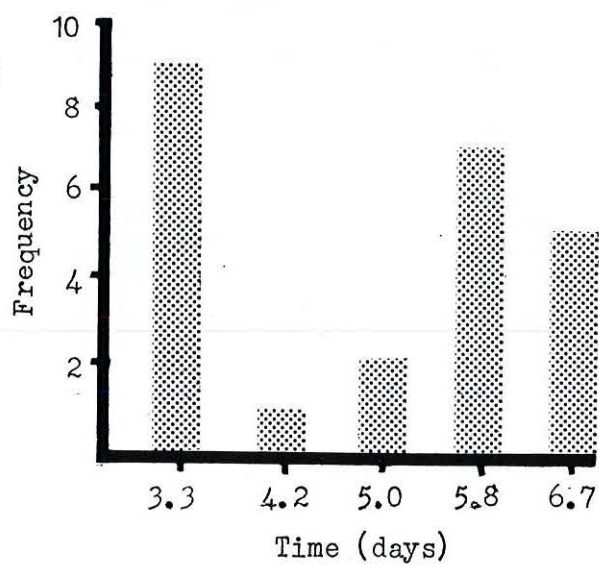
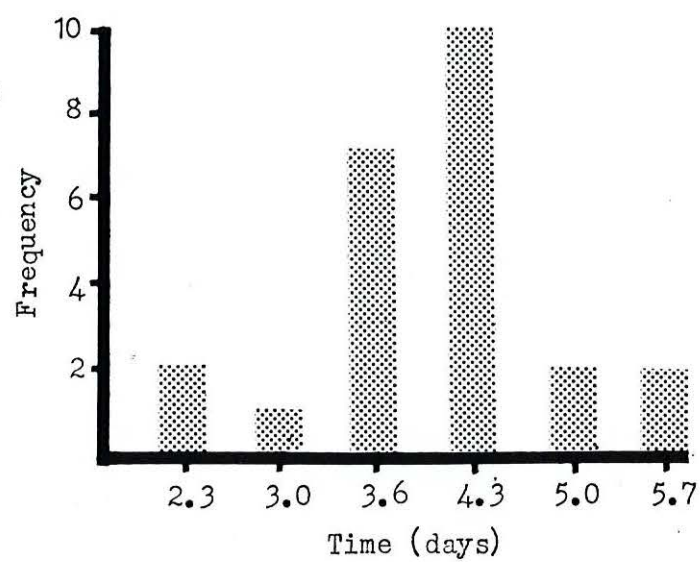
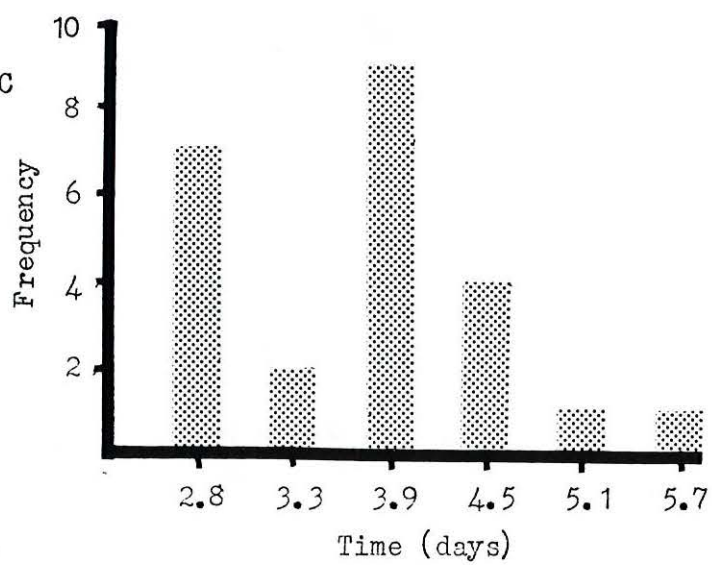
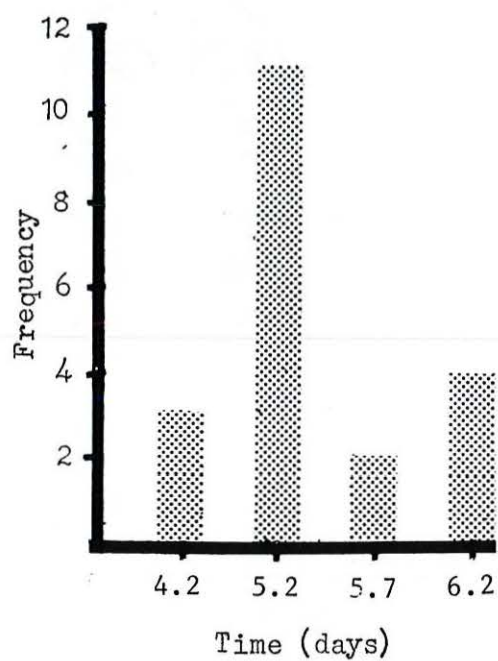
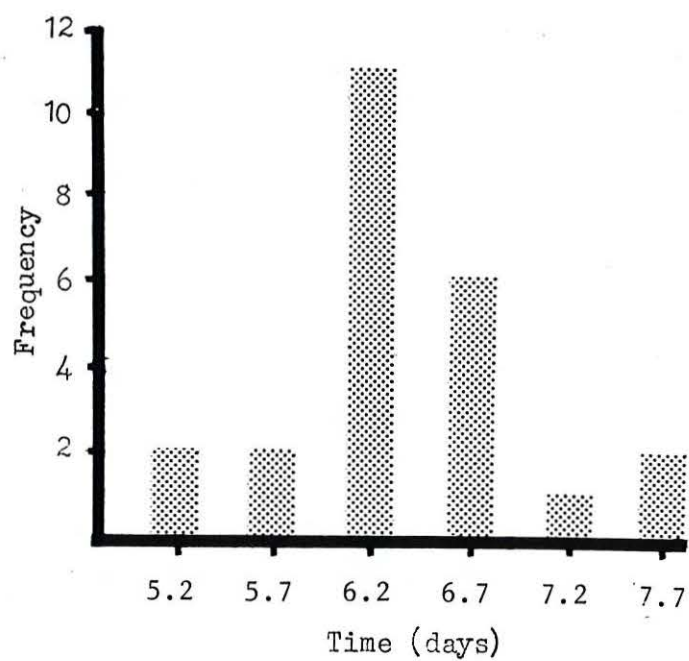
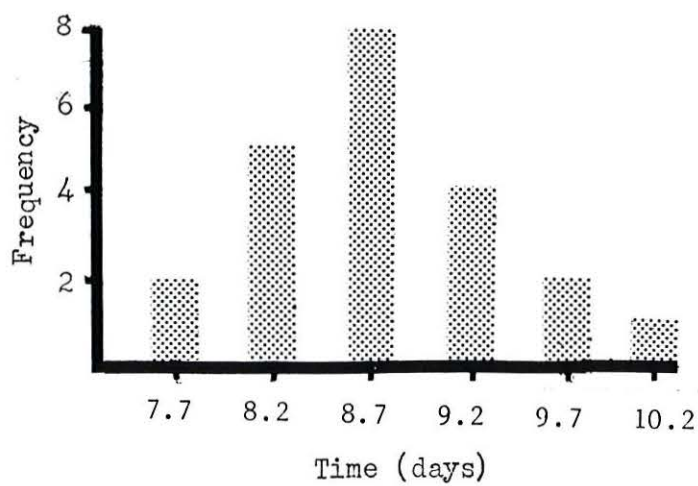
Fig. 3a: 22°CFig. 3b: 25°CFig. 3c: 28°C



Figure 4 - The frequency distribution of the pupal to eclosion stage of development for D. acutilabella at (a) 22°C, (b) 25°C and (c) 28°C.

Fig. 4c: 28°CFig. 4b: 25°CFig. 4a: 22°C

## DISCUSSION

In general ectotherms are known to undergo changes in lethal temperatures, rate functions, behavior and biochemical activities with different environmental temperatures. Three general time periods can be distinguished that may elicit some of these changes. Short term temperature changes (up to a few hours) at ambient temperatures which normally occur in the environment of the species directly affect the rate function. During long term exposure (up to days or weeks) the animal may compensate by acclimation. Over long periods of time genetic selection may occur (Prosser, 1973). It is the second kind of time period that is studied here. A useful classification of patterns of acclimation devised by Precht (in Prosser, 1973) describes the effect of temperature on rate processes in ectotherms as shown in Figure 5.  $T_2$  represents an intermediate temperature from which an animal is transferred to a lower temperature ( $T_1$ ) or a higher one ( $T_3$ ). The rate at the new temperature may rise and fall in direct response with no further changes as seen in Type 4. Type 2 indicates perfect compensation, i.e. the rate returns to the original value. Partial or incomplete acclimation is Type 3; excess compensation is Type 1; and inverse or para-

Figure 5 - Diagram of types of temperature acclimation according to Precht. Animals acclimated to  $T_2$  transferred to lower temperature  $T_1$ , or to higher temperature  $T_3$ .

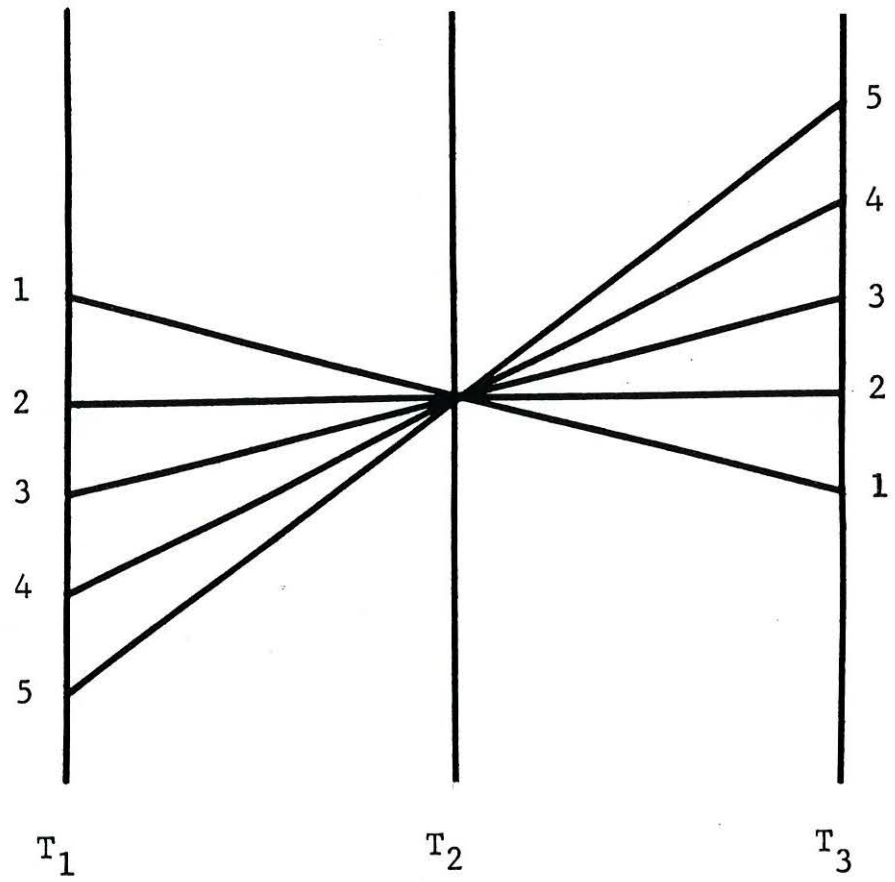


Figure 5

doxical acclimation is Type 5. According to this classification, the data for D. acutilabella is similar to Type 4 or Type 5.

The relationship between temperature and the duration of developmental stages has been studied in many species of insects (Rockstein, 1974). For example, Aedes completes development in 3.5 days at 15 C, 1.75 days at 20 C and in less than one day at temperatures above 25 C. Calandra completes its developmental cycle in 22 days at 15 C, in 10 days at 18 C and in less than 5 days at temperatures in the range of 20 to 33 C. This effect approximates an hyperbola, so that if the reciprocal of development duration (velocity) is plotted against temperature, an approximation to a straight line is obtained. Such is the case when development is studied under constant temperature. However, some experimenters have obtained an average rate of development under conditions of fluctuating temperature which is markedly different. During the sixties this effect was investigated by comparing development in constant and fluctuating temperatures (Rockstein, 1974). It was concluded "that if appropriate weightings are applied according to the precise form of the relation between temperature and developmental velocity, then the rate of development will



generally be the same whether constant or fluctuating temperatures are used" (Rockstein, 1974).

The experiment reported here was designed to investigate the effect of temperature on rate of development. Generally, the duration of developmental stages in insects falls steeply as temperatures are raised (Rockstein, 1974). The same is true for D. acutilabella, i.e. I observed a shorter developmental time for these flies at 28° C. There were significant differences between all the average overall life-spans at the three temperatures. However, when each stage at all temperatures was compared, I found that some differences were not significant. In the egg to larval stage there was no significant difference between the mean duration at 25° C and that at 28° C. The same was true for the larval to pupal and also the eclosion to sexual maturity stages at those temperatures. The differences in the durations at 22° C and those at 25° C are significant.

$Q_{10}$  varies over the temperature range and is higher in low ranges than in high ones, so that the temperature for which it is calculated must be specified (Prosser, 1973). In the rate of development of D. acutilabella the  $Q_{10}$  for 25° to 28° C was 33.3% lower than that for 22° to 25° C. If the optimal temperature for the development of D. acutilabella falls within the range of 25° to 28° C, this would be expected.

This study tests the hypothesis that Drosophila which inhabit a broad geographic area and live and breed over a wide temperature range are less affected by temperature changes, i.e. will have lower  $Q_{10}$  for developmental rate. D. melanogaster is an example of a widespread species. Suzuki (1970), followed its development over a temperature range (22° to 29°C) similar to that used here. The  $Q_{10}$  of development for D. melanogaster under these conditions was 1.8, slightly lower than the  $Q_{10}$  of 2.0 for D. acutilabella. This is to be expected when one considers the effect of temperature on biochemical reactions which determine the developmental rate. The  $Q_{10}$  of 1.8 indicates that the temperature change had less effect on D. melanogaster than on D. acutilabella. A comparison between another eurythermal species, D. simulans, and D. acutilabella shows a marked difference. D. simulans has a  $Q_{10}$  of 1.4 when reared at a range of 20° to 28°C (Mc Kenzie, 1978); a value 30% less than the value for D. acutilabella. In addition, D. nebulosa (20° to 30°C) and D. virilis (15° to 25°C), both eurytherms, have  $Q_{10}$ 's of 1.8 and 1.6, respectively (Nagatani, 1978). All four eurythermal species compared here have  $Q_{10}$  lower than D. acutilabella.

Other species of Drosophila have reactions to temperature similar to D. acutilabella. For example, Matzke's and Druger's (1977) results showed that D. pseudoobscura, a stenotherm whose normal habitat is cooler and in higher elevations, had a  $Q_{10}$  of 2.14 in a 16° to 25°C temperature range. It is interesting to compare this species with D. willistoni, a stenotherm living in hot climates. At 19° to 24°C, D. willistoni has a  $Q_{10}$  of 3.3. Finally, D. pavani has a  $Q_{10}$  of 2.3 for a range of 16° to 25°C (Budnik, et. al., 1971). All three species, in this case, have relatively higher  $Q_{10}$ 's than the eurytherms mentioned above.

Based on the data presented here, I conclude that the stenothermal species D. acutilabella has a higher  $Q_{10}$  than eurythermal species at temperatures near those of their natural habitat.

Had time permitted me to perform this experiment again, I would have taken several other factors into account. Population density may influence the rate of development and relative viability of species. Matzke and Druger (1977) found that crowding reduces viability and prolongs developmental time. Ideally, then, I should have had the same number of eggs in each vial. This would have ensured a balanced experimental design. There are



sexual differences within a particular species. McKenzie, in the same experiment mentioned previously, found that regardless of developmental temperatures, females live longer than males in D. melanogaster and D. simulans.

Bergmann's and Allen's rules predict that weight differences would occur between the adults eclosing at the three temperatures in this experiment, so that a dry weight analysis would have been useful (Ray, 1960). Other rate functions, such as oxygen consumption and glutamate-aspartate transaminase activity, have been demonstrated to be affected by temperature (Hunter, 1966, Burr, 1970). Perhaps it would be useful to compare  $Q_{10}$ 's of different functions within the same species, to have a broader look at the effect of temperature on the physiology of the organism.

## SUMMARY

The experiment reported here is designed to investigate the effect of temperature on the rate of development of D. acutilabella. The mean duration of the overall lifespan is  $17.0 \pm 0.8$  days at  $22^{\circ}\text{C}$ ,  $13.0 \pm 0.4$  days at  $25^{\circ}\text{C}$  and  $11.2 \pm 0.4$  days at  $28^{\circ}\text{C}$ .

The experiment tests the hypothesis that Drosophila which inhabit a broad geographic area and live and breed over a wide temperature range (eurythermal) are less affected by temperature changes than those which are limited in geographic distribution to narrower temperature ranges (stenothermal). When the  $Q_{10}$  of development of D. acutilabella, a stenothermal species, was compared to other eurythermal species, it was found that the results support the hypothesis.

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